# Physiological Modification of the Host Feeding Site by Cereal Aphids (Homoptera: Aphididae)

JOHN D. BURD[1]

Plant Science and Water Conservation Laboratory, USDA–ARS, 1301 N. Western Road, Stillwater, OK 74075

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**ABSTRACT** Indole-3-acetic acid-1-$^{14}$C and $^{14}$C-sucrose labels were used to study the effects of greenbugs, *Schizaphis graminum* (Rondani), and Russian wheat aphids, *Diuraphis noxia* (Mordvilko), on phloem function of wheat (*Triticum aestivum* L.). Greenbug feeding significantly reduced translocation from the immediate feeding site; however, phloem integrity was not impeded. In contrast, Russian wheat aphids had little effect on vein loading or phloem translocation at the feeding site. Similar results were obtained when resistant and susceptible wheats were infested with three different greenbug biotypes. Greenbugs fed artificial diets containing $^{14}$C-sucrose injected salivary material that was translocated to both root and shoot systems. The accumulation of salivary constituents in the roots of wheat seedlings fed upon by greenbugs may account for the significant reductions in root biomass that have previously been reported.

**KEY WORDS** *Schizaphis graminum*, *Diuraphis noxia*, *Triticum aestivum*, phloem translocation, vein loading, biotype

THE GREENBUG *Schizaphis graminum* (Rondani) is an important pest of wheat (*Triticum aestivum* L.) in the United States. Economic infestations occur annually and are primarily controlled by insecticides. Reliance on chemicals to control insect pests has led to environmental concerns which have stimulated research focusing on alternate methods of insect control. One alternative approach to greenbug management has been the development and use of resistant crops. However, the occurrence of new greenbug biotypes has been a major obstacle to the deployment of resistant wheat cultivars (see Porter et al. 1997). Therefore, it is important that a fundamental understanding of the mechanisms of greenbug damage be established to facilitate new approaches for seeking resistant plant sources.

Early cytological work by Chatters and Schlehuber (1951), focusing on greenbug damage at the feeding site, concluded that it is the injection of toxic saliva and not the uptake of food that is the primary cause of damage, and therefore, that greenbug resistance was physiological. This hypothesis agrees with ultrastructural studies of Saxena and Chada (1971), Al-Mousawi et al. (1983), and Morgham et al. (1994), who attributed greenbug resistance to biochemical and physiological factors. Moreover, Al-Mousawi et al. (1983) and Morgham et al. (1994) indicated that the visible damage (chlorosis/necrosis) at the feeding site is biochemically associated with the feeding track of the aphid. A biochemical basis of the feeding-site damage was presented in a review article by Dreyer and Campbell (1987). A model was portrayed in which salivary pectinases played the key role in the damage response.

Other greenbug-induced physiological changes in wheat have been reported. Ryan et al. (1987) found significant reductions in total chlorophyll, carbon assimilation rates, transpiration rates, and stomatal conductance in a susceptible wheat cultivar. Gerloff and Ortman (1971) reported similar results for greenbug susceptible barley (*Hordeum vulgare* L.). Dorschner et al. (1987) showed that significantly increased levels of free amino acids in greenbug-damaged susceptible wheat were closely correlated with the greenbug's ability to cause senescence-like damage at the feeding site.

Greenbugs feed from the phloem (Campbell et al. 1982), yet little is known of how the greenbug exploits this tissue. The objectives of this study were to determine the effects of greenbug feeding on phloem function at the feeding site and to evaluate the movement and accumulation within the plant of greenbug-injected salivary compounds. In addition, the effect of feeding by Russian wheat aphids, *Diuraphis noxia* (Mordvilko), on phloem integrity was compared with plant responses induced by greenbugs.

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[1] E-mail: jdburd@pswcrl.ars.usda.gov.

## Materials and Methods

**Experiment 1: Effect of Greenbug Feeding on Vein Loading and Phloem Translocation.** Pregerminated 'TAM W-101' winter wheat was planted in cone-tainers (Supercell Cone-Tainer, Ray Leach Cone-Tainer Nursery, Canby, OR), with one seed per container in a fritted clay medium (Absorb-N-Dry, Balcones Minerals, Flatonia, TX) (Burton 1986). Plants were grown in environmental chambers (Sherer model CE 38–15HLE, Rheem Manufacturing, Asheville, NC) at 21°C, 70 ± 10% RH, and a 16 h photophase. Plants were watered daily and beginning 7 d after emergence were fertilized biweekly with Peters' Peat-Lite Special (analysis 15-16-17) (Peters' Fertilizer Products, Fogelsville, PA), a water-soluble fertilizer. Fourteen days after planting, at growth stage 13 (Zadoks et al. 1974), 10 mature apterous biotype E greenbugs from greenhouse colonies, reared on 'Wintermalt' barley, were confined in a ventilated transparent plastic cage (3 by 3 by 1 cm) on aphid-treated plants (cf. Pathak and Painter 1958), 10 cm below the apical tip of the second leaf. Noninfested control plants were also caged at the same location and all cages were supported by wooden blocks to maintain the leaves at their natural position. The greenbugs were allowed to feed and reproduce for 7 d, after which the cages and aphids were removed.

In two separate tests, Indole-3-acetic acid (IAA)-1-$^{14}$C (57 mCi/mmol) and $^{14}$C-sucrose (560 mCi/mmol) (Amersham, Arlington Heights, IL) were used to assess the impact of greenbug feeding on phloem translocation. These labels were chosen because they are actively loaded into the phloem when applied to mature leaves (see Salisbury and Ross 1985). Label preparations were as follows: for the IAA-1-$^{14}$C test, 140 $\mu$l of IAA-1$^{14}$C was dried and added to distilled water to make 320 $\mu$l by adding 50% EtOH + 0.4% Triton X-100 (Sigma, St. Louis, MO), and for the $^{14}$C-sucrose test, 20 $\mu$l of $^{14}$C-sucrose was added to distilled water + 0.5% Triton X-100 to make 0.3 ml.

Labeling started 4 h after the onset of the photophase, and was done by placing four 2-$\mu$l droplets of the appropriate label on the adaxial surface of the previously caged 3-cm leaf section. Plants were harvested 4 and 8 h after application of the IAA-1-$^{14}$C and $^{14}$C-sucrose, respectively. Test plants were partitioned into four components, i.e., the apical tip of the treated leaf, the labeled 3-cm leaf section, the remainder of the shoot, and the roots; each plant part was then monitored for radioactivity.

The treated leaf sections were washed for 20 s in 50% EtOH. The partitioned samples were then lyophilized, ground in 5 ml of 100% EtOH, and 1 ml of each sample was counted in 15 ml of Complete Liquid Counting Cocktail (Research Products International, Mount Prospect, IL) using a Beckman liquid scintillation system (Beckman Instruments, Fullerton, CA). The experimental protocol for the test followed a paired-plot design where $n$ = 20; controls, $n$ = 10, infested, $n$ = 10.

**Experiment 2: Effect of Greenbug Feeding on Phloem Integrity.** To assess the impact of greenbug feeding on phloem integrity, aphids were allowed to feed and reproduce for 7 d on the caged leaf sections. Four hours after the onset of the photophase, 8 $\mu$l of $^{14}$C-sucrose label was incorporated into the apical portion of the caged leaf. Plants were harvested 4 h after labeling and were partitioned into treated leaf, shoot, and root components, then measured for radioactivity as described above. In addition, to the plant assays, the greenbugs were removed from the infested plants and measured for radioactivity. The experimental protocol followed a paired-plot design where $n$ = 20; controls, $n$ = 10, infested, $n$ = 10.

**Experiment 3: Effect of Different Greenbug Biotype and Russian Wheat Aphid Feeding on Vein Loading and Phloem Translocation in Resistant and Susceptible Host Plants.** Three biotypes of the greenbug, biotype B (GBB), C (GBC), and E (GBE), as well as the Russian wheat aphid, were evaluated in combination with greenbug resistant and susceptible wheat entries for their impact on phloem translocation. The plant entries tested were; TAM W-101, susceptible to GBB (Webster et al. 1986), GBC (Burton et al. 1985), GBE (Burton 1986) and the Russian wheat aphid (Webster 1990), 'Amigo', resistant to GBB and GBC but susceptible to GBE (Tyler et al. 1987) and the Russian wheat aphid (Bush et al. 1989), and 'Largo', resistant to GBC and GBE but susceptible to GBB (Tyler et al. 1987) and the Russian wheat aphid (Bush et al. 1989).

The plants were grown on greenhouse benches under natural light conditions (December–January). Otherwise, the materials and methods used were identical to those in experiment 1. Ten plants of each entry (growth stage 13, Zadoks et al. 1974) were infested with 10 aphids of one of the four aphid treatments, and 10 noninfested control plants were included per entry. The aphids were caged 10 cm from the apical tip of the second fully expanded leaf for 7 d, after which they were removed and counted. Next, 8 $\mu$l of the $^{14}$C-sucrose label was incorporated into the previously caged leaf section. Plants were harvested 4 h after labeling and were partitioned into treated leaf, shoot, and root components, and measured for radioactivity as described above. The experimental protocol followed a randomized complete block design, where $n$ = 50, treatments = 5, and blocks = 10, for each plant entry tested.

**Experiment 4: Translocation of Greenbug-Injected Saliva.** To evaluate the movement of salivary materials, greenbugs were fed for 72 h on an artificial diet labeled with $^{14}$C-sucrose. The artificial diet consisted of a 35% sucrose solution, with pH adjustment to 7.6 (Cress and Chada 1971) by adding 0.001 M KOH, combined with 600 $\mu$l of $^{14}$C-sucrose to make 10 ml of diet. The artificial diet was presented to the aphids in sachets made by sandwiching the diet solution between a stretched parafilm envelope (Mittler and Dadd 1964).

The greenbugs were then placed on a nontest plant (TAM W-101) for 24 h to allow the aphids time to clear the artificial diet from their stylets and gut. Next, the

**Table 1. Mean ± SE percentage of total $^{14}C$ exported from labeled leaf sections to different plant parts for infested and noninfested TAM W-101 wheat seedlings**

| Plant part | % recovery of applied label | |
|---|---|---|
| | $^{14}C$-IAA | $^{14}C$-sucrose |
| Apical tip | | |
| Infested | 1.0 ± 0.7 | 1.1 ± 0.2 |
| Control | 0.9 ± 0.2 | 1.2 ± 0.2 |
| Treated section | | |
| Infested | 96.2 ± 12.4* | 62.5 ± 9.6* |
| Control | 71.9 ± 10.1 | 28.4 ± 7.8 |
| Shoot | | |
| Infested | 1.3 ± 0.3* | 3.8 ± 0.9* |
| Control | 17.8 ± 3.2 | 10.9 ± 1.4 |
| Root | | |
| Infested | 1.3 ± 0.4* | 32.6 ± 5.3* |
| Control | 9.4 ± 0.9 | 59.5 ± 11.8 |

Plant part means within a column followed by an asterisk were significantly different, $P \leq 0.05$, paired *t*-test.

aphids were transferred from the nontest plants to TAM W-101 wheat seedlings (growth stage 13, Zadoks et al. 1974) for evaluation. Fifteen greenbugs were caged on each plant 10 cm from the apical tip of the second fully expanded leaf. The test plants ($n = 24$) were grown under the same environmental conditions as described for experiment 1. The greenbugs were allowed to feed and reproduce on the plants for 7 d, after which they were removed, and the plants were harvested and measured for radioactivity as described above. The plant parts measured were the leaf above the feeding site, the feeding site, the leaf below the feeding site, the remainder of the shoot, and the roots.

**Statistical Analysis.** The amount of radioactivity within each plant part was expressed as a percentage of total radioactivity recovered (excluding the labeled leaf wash). Data analysis and computations were done with SAS (SAS Institute 1988). The *t*-test procedure was used for all statistical tests in experiments 1 and 2. Data from experiment 3 were analyzed using the analysis of variance (ANOVA) procedure and means were separated using Tukey's studentized range test ($P \leq 0.05$, SAS Institute 1988).

## Results and Discussion

Greenbug feeding significantly reduced the amount of $^{14}C$ exported to both root and shoot partitions from mature leaves (Table 1). The phloem translocation of exogenous IAA after application to mature tissue has been shown to readily occur (see Ziegler 1975) and in our study, exported $^{14}C$ recovered from IAA-1-$^{14}C$ treated leaf sections accounted for ≈28% of the total percentage of label recovered in noninfested plants compared with <4% for those infested with aphids. Translocation of sucrose, which is the principal sugar translocated in the phloem (Geiger 1975), was significantly reduced. The $^{14}C$-sucrose exported from the leaf sections on noninfested plants accounted for ≈71% of the total radioactivity recovered compared with ≈37% for infested plants. Despite this 50% decrease in the amount of $^{14}C$-sucrose translocated from infested leaves, carbohydrate partitioning patterns were not altered. When compared with noninfested controls, the proportion of $^{14}C$-sucrose allocated to the root and shoot partitions was not significantly changed.

Phloem blockage caused by aphids has been reported (Wood et al. 1985) and potentially could account for the observed decrease in phloem loading. However, phloem translocation of $^{14}C$-sucrose was not impeded by greenbugs that were caged downstream from the labeling site and as before the pattern of sucrose partitioning to the root and shoot was not altered (Table 2).

Both IAA and sucrose are actively loaded into the phloem of mature leaves (Giaquinta 1983, Bandurski and Nonhebel 1984). Electrogenic proton pumps, probably membrane-bound ATPase complexes, serve as the active vein loading system by creating a pH generated transmembrane electrochemical gradient that is coupled to a carrier-mediated co-transport system (Marschner 1986, Spanswick 1981). Because IAA and sucrose do not share the same protein carrier (Kursanov 1984), the data suggest that the inhibition of vein loading caused by greenbugs may result from a localized inactivation of the electrogenic pump system. Moreover, phloem loading of amino acids, which is also coupled to the proton-motive force arising from these electrogenic pumps (Reinhold and Kaplan 1984), would be similarly impacted, and the efflux of amino acids from the greenbug feeding site should be reduced. Evidence for a greenbug induced inhibition of amino acid efflux was reported by Dorschner et al. (1987) who observed that greenbugs caused the amount of free amino acids in mature wheat leaves to significantly increase at the infestation sites.

In a subsequent experiment, the effect of different greenbug biotypes and the Russian wheat aphid on vein loading in resistant and susceptible wheats was investigated. Aphid population growth on the different wheat entries is shown in Table 3. Compared with the greenbug biotypes, the mean number of Russian wheat aphids was generally lower, and may be attributable to an inherently lower reproductive rate (Webster and Starks 1987). Population means for GBB were significantly lower than those of GBC and GBE on TAM W-101 (GBB susceptible) and Amigo (GBB resistant). Nonetheless, GBB caused a substantial amount of visible damage to TAM W-101.

**Table 2. Mean ± SE percentages of total $^{14}C$ incorporated into apical tip of greenbug biotype E infested and noninfested TAM W-101 wheat seedlings that were recovered from different plant parts**

| Plant part | % recovery of applied label | |
|---|---|---|
| | Infested | Control |
| Treated leaf | 76.6 ± 15.1NS | 81.7 ± 10.9 |
| Shoot | 3.9 ± 0.6NS | 2.9 ± 0.8 |
| Root | 13.3 ± 7.3NS | 15.3 ± 4.1 |
| Greenbug | 6.2 ± 1.8 | |

Plant part means within a row followed by NS were not significantly different, $P \leq 0.05$, paired *t*-test.

**Table 3. Mean ± SE number of aphids per plant**

| Aphid type | Plant cultivar | | |
|---|---|---|---|
| | TAM W-101 | AMIGO | LARGO |
| Greenbug biotype B | 38.1 ± 10.6b | 56.4 ± 12.9b | 62.8 ± 15.2a |
| Greenbug biotype C | 100.5 ± 21.4a | 102.2 ± 16.8a | 50.9 ± 9.7a |
| Greenbug biotype E | 97.4 ± 16.5a | 100.6 ± 14.6a | 63.3 ± 17.4a |
| Russian wheat aphid | 30.5 ± 16.3b | 36.8 ± 11.1b | 24.3 ± 6.4b |

Column means followed by a different letter were significantly different, $P \leq 0.05$, Tukey's test.

On the susceptible wheat entries, virulent greenbug biotypes induced a characteristic phytotoxic response, that initially appeared as small necrotic lesions (<1 mm diameter) surrounded by chlorotic halos (Al-Mousawi et al. 1983, Puterka and Peters 1988). As the greenbug populations increased, the chlorotic halos coalesced, and on some plants, the entire caged section became chlorotic. However, the chlorosis was restricted to the feeding site and never extended beyond the boundary of the cage. Greenbug resistant wheats did not exhibit pronounced visible symptoms, necrotic lesions did not occur and visible damage was limited to an occasional chlorotic spot (<1 mm diameter). Visibly, damage caused by Russian wheat aphids differs from that of greenbugs and is typified by the development of longitudinal white streaks on infested leaves (Walters et al. 1980). In this study, Russian wheat aphids caused considerable chlorosis on all wheat entries tested. However, no leaf streaking or necrosis was observed.

Based on the percentage of translocated $^{14}$C-sucrose recovered, all greenbug biotypes significantly decreased vein loading in all wheat entries tested, and the pattern of this reduction was consistent among the different plant entries (Table 4). The fact that vein loading was inhibited on both resistant and susceptible entries, irrespective of the greenbug biotype, suggests that this plant response occurs independent of the visible damage symptoms. In contrast to greenbugs, Russian wheat aphids had no impact on vein loading, and the percentage of $^{14}$C-sucrose translocated did not differ significantly from noninfested controls.

Aphids can alter host tissues, and therefore nutrient availability, in the immediate vicinity of the feeding site (Way and Cammell 1970, Dixon and Wratten 1971). The ability of greenbugs and Russian wheat aphids to cause senescence-like damage at the feeding site has been associated with substantial increases of free amino acids. These are thought to enhance the diet quality of the plant (Telang et al. 1999, Sandstrom et al. 2000) and in turn result in increased aphid fitness (Dorschner et al. 1987). Results from the present studies indicate that greenbugs also significantly reduce the rate of phloem loading, which could further benefit the aphid by the retention and accumulation of essential amino acids at the feeding site of susceptible plants. Further evidence for this response is the accumulation of starch granules in the chloroplasts of resistant wheat reported by Morgham et al. (1994) which would result from the local accumulation of photosynthates.

**Table 4. Mean ± SE percentage of recovered $^{14}$C-sucrose translocated from the feeding site of aphid infested and noninfested resistant and susceptible wheat seedlings**

| Aphid type | Plant cultivar | | |
|---|---|---|---|
| | TAM W-101 | AMIGO | LARGO |
| Greenbug biotype B | 2.7 ± 1.4b | 2.0 ± 1.1b | 0.6 ± 0.3b |
| Greenbug biotype C | 1.1 ± 0.9b | 1.0 ± 0.8b | 2.6 ± 1.2b |
| Greenbug biotype E | 2.0 ± 1.5b | 0.6 ± 0.5b | 1.8 ± 1.2b |
| Russian wheat aphid | 11.5 ± 1.3a | 9.6 ± 3.4a | 12.4 ± 1.8a |
| Non-infested control | 12.5 ± 3.2a | 17.0 ± 3.9a | 15.7 ± 2.6a |

Column means followed by a different letter were significantly different, $P \leq 0.05$, Tukey's test.

**Table 5. Mean ± SE percentage of total $^{14}$C recovered from different plant parts of TAM W-101 wheat seedlings following infestation with radiolabeled aphids**

| Plant part | % recovery of applied $^{14}$C label |
|---|---|
| Infested leaf | |
| Feeding site | 42.9 ± 9.1 |
| Leaf tip | 4.8 ± 1.3 |
| Leaf base | 13.1 ± 2.4 |
| Shoot | 9.4 ± 3.7 |
| Root | 29.8 ± 7.2 |

It is generally thought that plant damage caused by greenbugs results from a toxin-like substance that is injected into the plant during feeding (Chatters and Schlehuber 1951, see Miles 1999). We used greenbugs that were radiolabeled with $^{14}$C-sucrose to identify the presence of salivary materials in the host tissues. Our results showed that greenbug saliva was injected into the plant and was translocated to both root and shoot tissues (Table 5). The majority of the injected material, ≈61%, was found in the infested leaf, while ≈30% was recovered from the roots. Although greenbugs cause substantial damage to the aerial portions of the plant, significant damage, in terms of biomass reduction, also occurs in root systems (Ortman and Painter 1960, Daniels 1965, Burton 1986). Moreover, Holmes et al. (1991) reported that the damage to roots caused by greenbugs is not the direct result of depleted photosynthate pools. Consequently, the present data suggest that the greenbug salivary materials translocated to the roots may be responsible for inducing a phytotoxic response that results in seedling root damage.

In conclusion, feeding by greenbugs and Russian wheat aphids did not occlude phloem tissue and phloem translocation through the feeding site was not disrupted. However, evidence was found that demonstrates the capacity of greenbugs to manipulate their feeding site by inhibiting vein loading and thereby making it potentially more nutritious for a protracted period of time. Moreover, it is apparent that this is a second site of action because it occurs in both resistant and susceptible wheat and is independent of the visible chlorotic-damage response. Further research is needed to characterize the mechanism(s) that regulate this response to aid in plant resistance development.

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